

Ant-plants as oases: Colonies of *Cladomyrma sirindhornae* (Hymenoptera, Formicidae) thrive in their host plants *Sphenodesme pentandra* in both the wet and dry seasons

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Abstract

Seasonal changes affect the distribution and behavior of animals. Ant societies are strongly affected by the dry season: they suffer from high temperatures and desiccation, but also from the lower availability of insect prey. However, some species of ants are involved in mutualistic relationships with myrmecophytic plants that provide a moist nesting space and nutrition. The effects of seasonal changes on such ant-plant symbioses are poorly understood. In this study, we report the nesting habits, colony composition and reproductive status of a plant-ant species, *Cladomyrma sirindhornae* Jaitrong, Laedprathom & Yamane, 2013 in the wet and dry seasons in Thailand. *C. sirindhornae* nested inside vines of *Sphenodesme pentandra* Jack, a pioneer species found in secondary dry evergreen forests and at forest edges which provides naturally hollowed stems for ant colonies. Among the 243 observed vines in this study, 223 vines (92%) were inhabited by *C. sirindhornae* while only 11 (4.5%) were occupied by other ant species, suggesting a high specialization of the ant-plant mutualism. *C. sirindhornae* nested within the cavities of the host plant, extending throughout the stems and

branches from the base to the canopy. A comparison of ten colonies collected in the dry season and ten in the wet season showed no effects of seasonality on colony size and proportion of larvae, worker pupae and scale insects. However, sexual pupae and adults were more abundant in the wet season than in the dry season. Our results suggest that myrmecophytes buffer seasonal variations, allowing plant-ant colonies to grow year-round, while reproductives are produced only when conditions outside are favorable for colony founding.

Keywords

Cladomyrma, Formicinae, myrmecophyte, nesting habitat, phragmosis, plant-ants, seasonality

Introduction

Seasonal climatic factors, such as variations in temperature, humidity, and precipitation, influence insect diversity in tropical and temperate ecosystems by affecting the availability of resources and the ecological conditions (Wolda 1988). In ecosystems with marked seasonality, the abundance of most insect orders decreases in the dry season (e.g. Janzen 1973; Pinheiro et al. 2002; Vasconcellos et al. 2010). Ant activity is influenced by environmental conditions. Kaspari and Weiser (2000) report that foraging ants avoid desiccation: in that study, ant activity increased by 200 percent along habitat moisture gradient, 25 percent from dry to wet seasons and 15 percent from day to night. This pattern indicates that the ants forage less during the dry season (Kaspari and Weiser 2000; Chantarasawat et al. 2013). However, Moses et al (2023) report region-specific responses to seasonality, with higher ant activity during the dry season in Papua New Guinea and Tanzania, but not in Ecuador. The foraging activity of ant workers is influenced by the resource abundance, brood production, physiological adaptation to ambient temperature, humidity and luminosity (Hölldobler and Wilson 1990). Importantly, ant larvae need proteins (amino acids) for their development (Abbott 1978, Stradling 1978). Therefore, ant colonies also suffer from the common decrease of insects during the dry season, in particular predatory and scavenger species that exclusively feed on other arthropods. For example, ground-dwelling *Cerapachys sulcinodis* rarely forage and pause reproduction as a response to low arthropod density during the dry season in Thailand (Mizuno et al. 2019). The impact of seasonality on colony composition in tropics has been studied in a few other ant species e.g. *Solenopsis geminata* (Helms and Vinson 2008) and *Pheidole ceres* (Judd 2005), but overall, such reports remain scarce.

Among the various examples of mutualism between ants and plants, ant-myrmecophyte (or ant-plant) symbioses are remarkable. Myrmecophytes provide hollow nesting spaces called domatia to host plant-ants (Fiala and Maschwitz 1992; Davidson and McKey 1993). Some host plants can also attract ants by providing nutrition through nutrient-rich food bodies, extrafloral nectar, or honeydew through sap-feeding insects (Huxley and Cutler 1991; Sandler and Dixon 2008). *Sphenodesme pentandra* Jack, the only known host of *Cladomyrma sirindhornae* ants (Jaitrong et al. 2013), is a climbing plant of the family Verbenaceae. Note that Jaitrong et al. (2013) initially misidentified the host plant of *C. sirindhornae* as *Sphenodesme involucrata* (C. Presl) B. L. Rob. This pioneer plant species

is distributed in India, Laos, Cambodia, Thailand, Malaysia and Burma (Chuakul et al. 2002; Wiart 2006), typically inhabiting secondary dry evergreen forests and forest edges. Some plants in the family Verbenaceae are known to provide nectar and/or food bodies to ants (Blüthgen and Reifenrath 2003). For example, *Clerodendrum fistulosum* (Verbenaceae) is one of the earliest documented myrmecophytes, characterized by the presence of domatia inhabited by ants (Beccari 1884). In Sarawak, it forms an obligate association with *Camponotus* (*Colobopsis*) *clerodendri* Emery. The lower surface of *C. fistulosum* young leaves is dotted with numerous nectaries, which appear as green spots on a reddish background and secrete glucose-rich nectar, although it does not produce specialized food bodies (Maschwitz, Fiala, and Linsenmair 1994). Similar information on domatia structure and presence of extrafloral nectar (ENF) and/or food bodies is, however, lacking for *Sphenodesme pentandra*.

Cladomyrma (Formicinae: Plagioleptini, Boudinot 2015) is a genus of plant-ants comprising thirteen species endemics to the Oriental tropics. These ants are known to nest inside the living shoots, stems, and branches of various myrmecophyte species and tend scale insects for honeydew (Moog 2009). While some species are found in humid tropics with no marked seasonality like *C. maschwitzi* in West Malaysia (Moog et al. 1998), others are confronted to a strong dry season like *C. sirindhornae* in eastern Thailand with temperature at 35.0–39.9 degrees Celsius and humidity at 71–74% (Jaitrong et al. 2013; Thai Meteorological Department 2025).

To understand the consequences of the dry season on an ant-myrmecophyte mutualism, we investigated the nesting habits, colony composition and reproductive status of *C. sirindhornae* in Thailand during wet and dry seasons in *Sphenodesme pentandra* host plants. We hypothesized that the colonies will be smaller and less reproductively active in the dry than the wet season.

Methods

Nesting habits and colony collection

We investigated the nesting habits of *C. sirindhornae* by sampling of *S. pentandra* Jack plants from various habitats, including secondary forests, forest edges, and forest paths in central and eastern Thailand. A total of 243 *S. pentandra* vines were randomly collected from 243 separate host trees to examine the existing ant species in the cavities. Each vine was collected from the host tree spaced at least 10 meters apart to ensure that vines from the same ant colony were not sampled more than once (i.e., each nest chamber represented a different colony). The vines were put in plastic bags and transported to the laboratory. In the laboratory, the vines were cut open to identify the ant species nesting within the cavities. These vines were collected from four sites: Nong Pla Subdistrict, Mueang District, Saraburi Province (14.440535°N, 100.95984°E); Mueang District, Nakhon Nayok Province (14.324434°N, 101.308769°E); Tok Prom Subdistrict, Khlung District, Chanthaburi Province (12.631996°N, 102.322258°E); and Tha Mai District, Chanthaburi Province (13°02'54"N, 101°10'59"E).

Colony composition

From the above 243 vines, we collected twenty colonies of *C. sirindhornae* and brought them to the laboratory for dissection to investigate the colony composition by counting the number of alate queens, males, workers, and brood (worker pupae, sexual pupae, and larvae separately counted). The colony condition (queenright or queenless) was also scored accordingly (the dealate queen present or not). Six out of the 20 colonies were collected from Tok Prom Subdistrict, Khlung District (colony code: WJT110214-1, WJT110214-2, WJT120214-1, WJT030214-1, WJT030214-2, WJT040214-1), Chanthaburi Province, and fourteen colonies were collected at Tha Mai District, Chanthaburi Province (colony code: C1, C2, C3, C4, C5, C6, C7, C8, C9, C10, C11, C12, C13, C14). The collection was carried out in February 2014 and March 2018 for the dry season, and in August 2014 and June 2018 for the wet season. We cut the entire plant, from the bottom of stem to the top of branches, to make sure that the whole colonies of *C. sirindhornae* were collected. We ensured that each plant was separate by 10 meters to avoid collecting ants from the same colony. Additionally, the length of each host plant collected from Tha Mai District, Chanthaburi Province (colony code: C1–C14) were measured and the number and diameter of nest entrances were recorded.

Ovary dissection and head width measurement

The reproductive condition of dealate queens from 13 out of 20 colonies (queenright colonies) were dissected under a stereo microscope immediately after collection and compared between the two seasons. We recorded the number of ovarioles and developing oocytes in each dealate queen. Furthermore, the head widths of 18 alate queens and 121 workers (61 major workers and 60 minor workers) from one colony were measured using an ocular micrometer on a stereo microscope to assess worker morphology in relation to nest entrance sizes.

Statistics

The relative abundance of sexual adults, sexual pupae, worker pupae, larvae and scale insects was computed for all the host plants as the ratio between the number of individuals divided by the total number of workers in the colony and compared between the wet and dry season by using the Mann–Whitney *U* test. The head width of alate queens, major workers, and minor workers were compared between castes within one nest using the Kruskal–Wallis test. The Generalized Linear Mixed Model (GLMM) with a Poisson distribution and a log-link function was utilized to examine the effects of seasonality and plants length on colony size (i.e., for plants C1–C14 only where length data measured), including the number of reproductive, number of major and minor workers. The seasonality and plants length were selected as fixed variables and colony identity was selected as a random variable to account for colony-specific variation in colony size. The model was fitted using the “glmer” function from the “lme4”

package in R (Bates et al. 2015). We plotted individual data points to show how colony size varied with plant length and season. The smooth curves were added using `geom_smooth`, which plots the predicted values based on the fitted Poisson GLMM. All statistical analyses were performed using R Studio, version 4.3.2.

Results

Nesting habits

We identified *Sphenodesme pentandra* Jack as a host plant of *Cladomyrma sirindhornae*. Out of 243 observed *S. pentandra* vines, *C. sirindhornae* nested inside the cavity of 223 vines (91.8%). Of the remaining vines, 11 (4.5%) were occupied by other ant species (e.g. *Cataulacus granulatus*, *Crematogaster* sp., *Pheidole* sp., *Pseudolasius* sp., *Tapinoma* sp., and *Tetramorium* sp.) and 9 (3.7%) vines were not used by any ants. *Cladomyrma sirindhornae* nested in domatia throughout the stems and branches of the host plant from the base to the canopy. The ant workers did not excavate tunnels inside the host plant by themselves. Instead, the host plant naturally forms cavities along its branches. These cavities continue until they reach the tip of the branch, which becomes narrow and prevents further cavity formation. As a result, ants are not found inhabiting these areas (Fig. 1). Furthermore, we found numerous food bodies resembling soft, light orange gel within the domatia (Fig. 1). These food bodies were abundantly distributed throughout the domatia, and worker ants actively transport them (personal observation). Nevertheless, we did not find any extrafloral nectaries in *S. pentandra*.

The average length of the *S. pentandra* vines was 16.9 ± 3.4 m (mean \pm SD), ranging from 11.8 to 21.3 m. Along the stems of the host plant, 97 ± 18 small elliptical nest entrances were found. Entrance holes had a diameter of 0.72 ± 0.21 cm and were located 1.5 ± 0.2 cm under a branch or leaf and 15.7 ± 2.6 cm apart from each other (Fig. 1). Major workers often blocked these holes with their heads (phragmosis, Fig. 2C). Dealate queens were found at swollen parts of the stem, 3 to 12 meters away from the vine base. Adults and brood of *C. sirindhornae* were observed throughout the cavities of the host plant from the base to the canopy. Similarly, scale insects of the family Pseudococcidae were found throughout the host plant domatia, cohabiting with *C. sirindhornae* (Fig. 2D).

Caste polymorphism

Thirteen dealate queens were dissected immediately after being collected from the field. These dealate queens had 32 ± 4 ovarioles per individual (mean \pm SD) in both the dry and wet seasons, characterized by dense yellow bodies and oocytes. The number of developing oocytes in the dry season (244 ± 44 , $N = 7$) was not different from that in the wet season (300 ± 112 , $N = 6$) (Welch two sample *t*-test, $t = -1.15$, $df = 6.36$, $p = 0.29$). The spermatheca was large and ellipsoidal (Fig. 3). Both major ($N = 17$) and minor ($N = 18$) workers had two ovarioles (1:1), with a few developing mature oocytes.

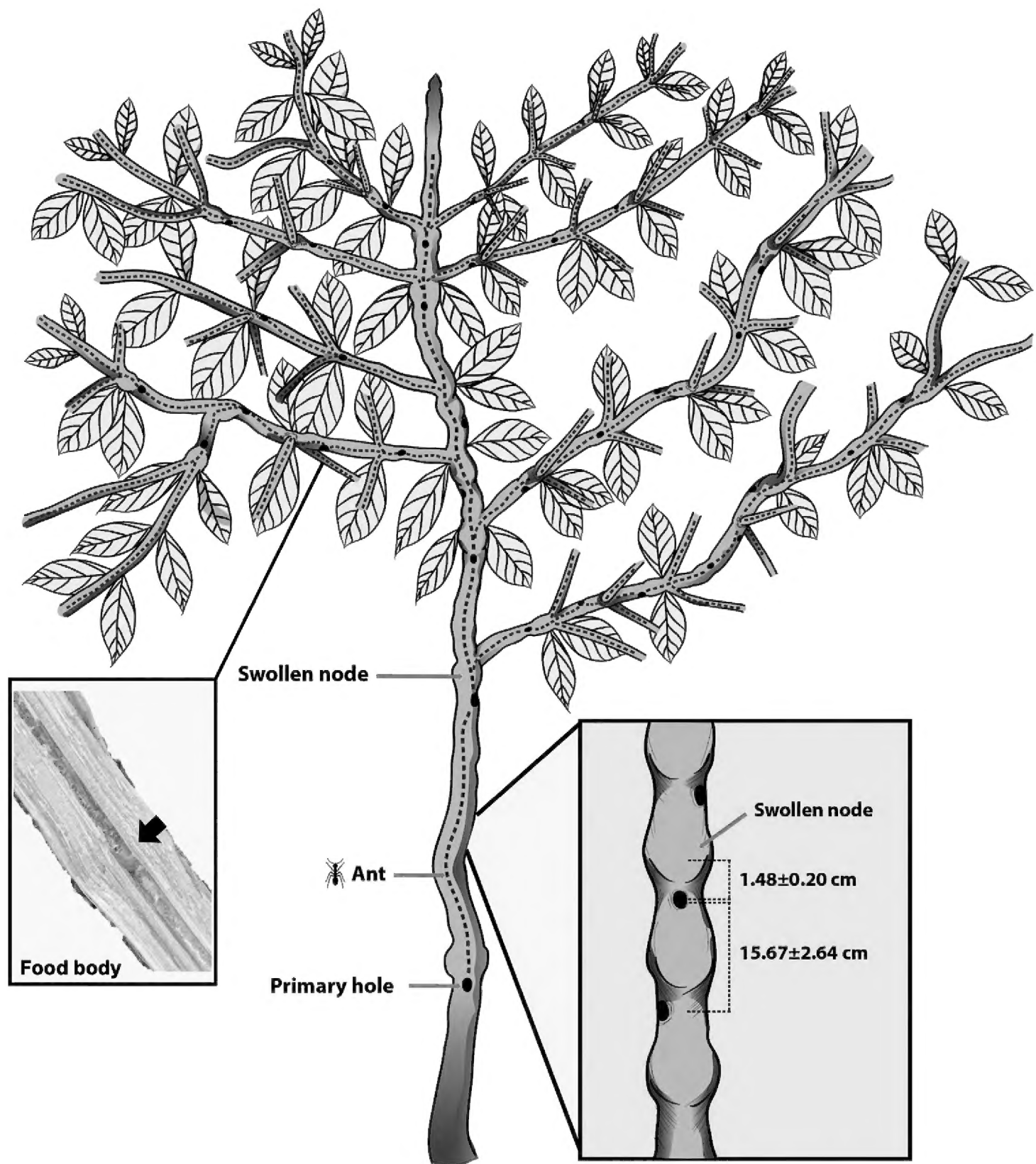


Figure 1. Nest structure of *Cladomyrma sirindhornae* on *Sphenodesme pentandra* Jack. The ants use cavities throughout the stem and branches of the host plant from the base to the canopy. The food bodies resembling soft, light orange, gel-like masses were found distributed throughout the domatia.

The head width of alate queens ranged from 0.93 to 1.00 mm (Fig. 4). Major workers exhibited a similar head width range (0.91 to 1.00 mm), while minor workers had a significantly smaller head (0.60 to 0.70 mm) (Kruskal-Wallis test, $p < 0.001$). Minor workers were often observed using small nest entrances to go in and out that major workers sealed with their head (phragmosis). The head width of minor workers (0.64 ± 0.03 mm) was smaller than the diameter of most entrance holes (0.89 ± 0.19 mm, ranging from 0.50 to 1.10 mm). In contrast, major workers and queens, in virtue of their large head, likely used only the largest holes to exit.

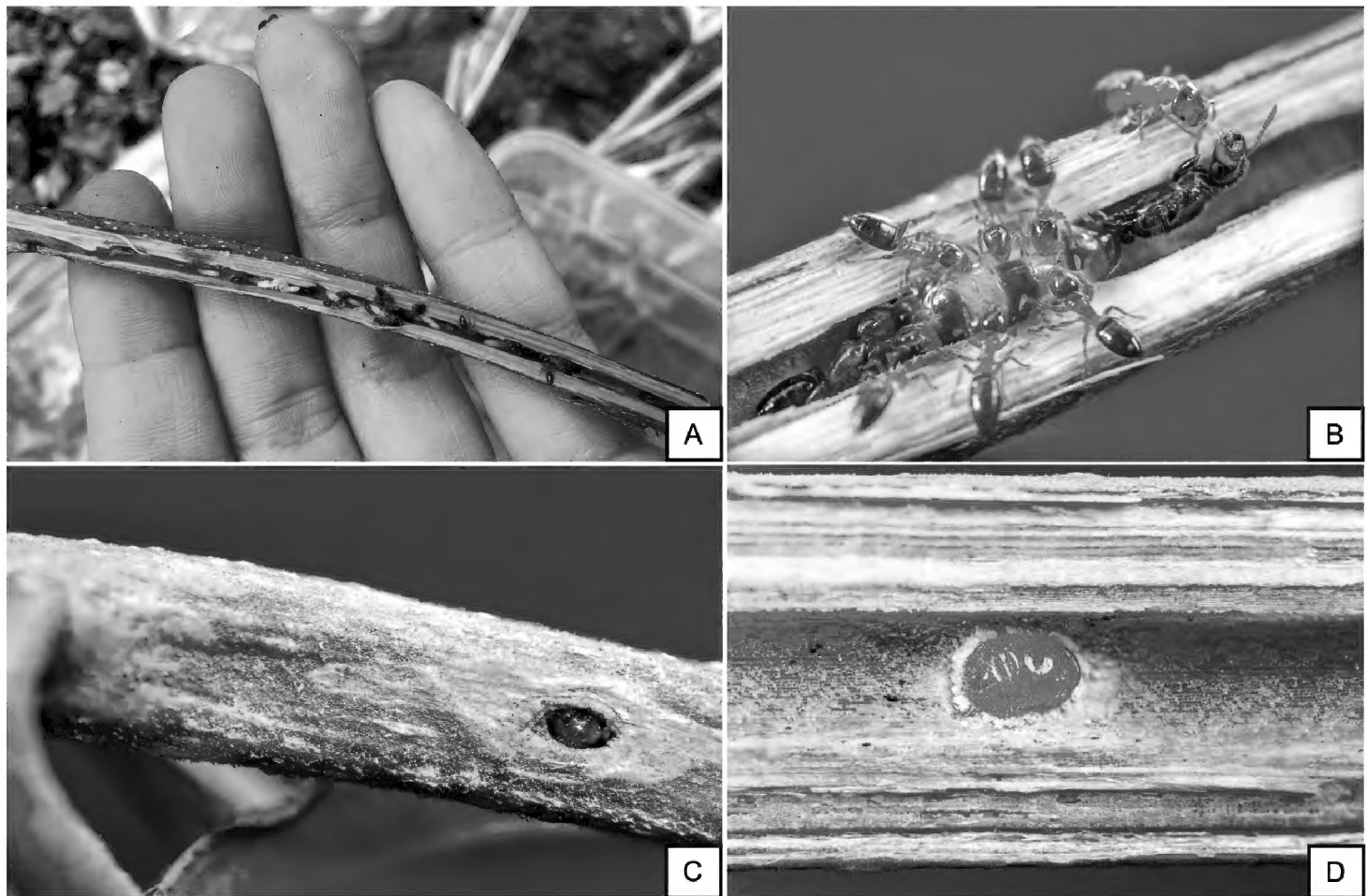


Figure 2. Nesting habit of *C. sirindhornae* **A** *C. sirindhornae* nesting inside a hollow branch of *S. pentandra* (photo by Sunittra Aupanun) **B** workers grooming the dealate physogastic queen (photo by Krittanun Tantraporn) **C** major worker blocking an entrance hole with its head (photo by Krittanun Tantraporn) **D** scale insects were found in all colonies of *C. sirindhornae* (photo by Krittanun Tantraporn).

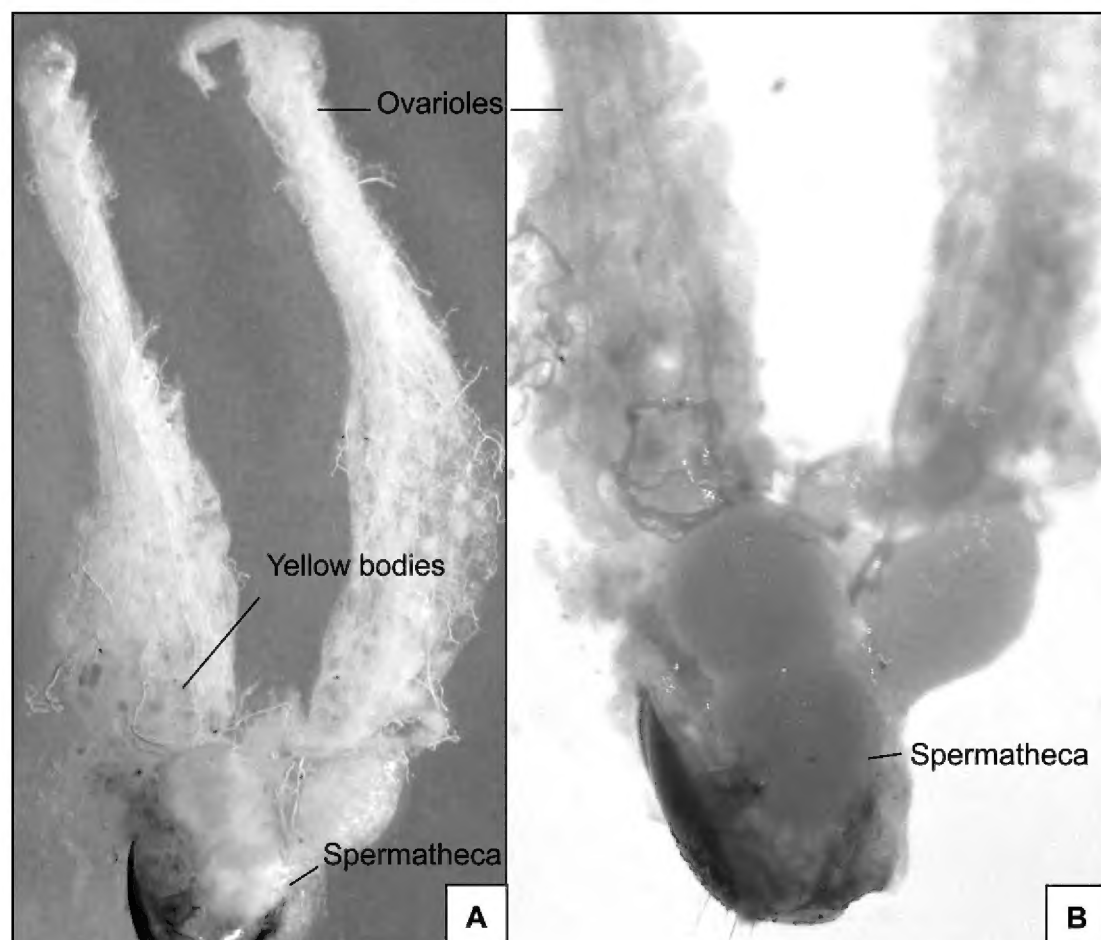


Figure 3. Ovaries of a dealate queen of *C. sirindhornae* (photo by Sunittra Aupanun) **A** whole ovary (photo by Sunittra Aupanun) and **B** spermatheca and basal oocytes (photo by Sunittra Aupanun).

Colony composition

The colony composition of all twenty colonies of *C. sirindhornae* is displayed in Table 1. Thirteen were queenright with a single dealate queen, while seven were queenless. All dealate queens were highly physogastric (Fig. 2B). All but one colony

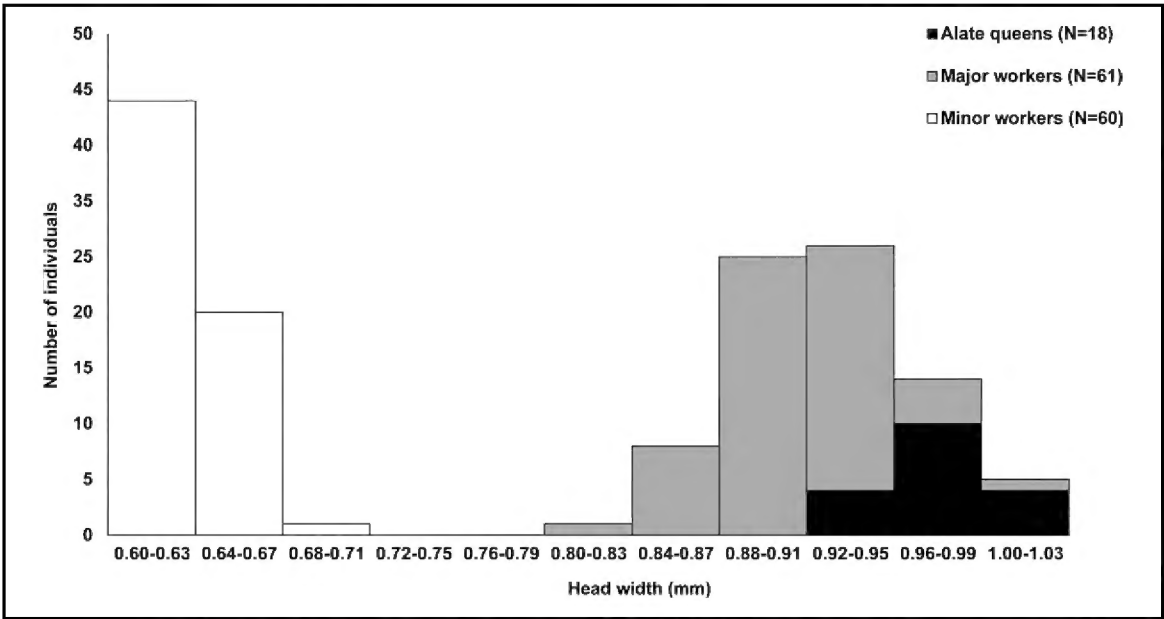


Figure 4. Head width distribution of *C. sirindhornae* alate queens and workers.

Table 1. Colony composition of *Cladomyrma sirindhornae*. RE: reproductives (alate queens and males).

Colony code	Date	Dealate queen	Alate queens	Males	Workers (Major)	Workers (Minor)	Pupae (worker)	Pupae (RE)	Larvae	Scale insects	Plant length (m.)
Dry season											
WJT110214-1	11 Feb. 2014	1	26	17	449	1810	159	74	96	48	-
WJT110214-2	11 Feb. 2014	1	144	5	572	2537	139	163	298	43	-
WJT120214-1	12 Feb. 2014	1	47	0	280	2998	33	39	254	82	-
C1	16 March 2018	1	0	9	1285	2657	472	6	211	229	10.24
C2	16 March 2018	0	0	0	887	2074	448	3	256	174	7.75
C3	16 March 2018	1	1	9	1139	2003	457	4	331	141	10.71
C4	17 March 2018	1	50	2	3217	8533	1740	27	1555	46	14.12
C5	17 March 2018	0	10	190	476	2268	386	206	692	317	15.54
C6	17 March 2018	0	17	11	2176	8554	1580	13	1139	243	8.5
C7	17 March 2018	1	1	6	2623	6291	1217	8	2192	179	8.72
Mean			29.6	24.9	1310.4	3972.5	663.1	54.3	702.4	150.2	10.8
± SD			± 44.41	± 58.25	± 1019.90	± 2727.83	± 617.80	± 72.68	± 702.98	± 95.20	± 2.96
Wet season											
WJT030214-1	3 Aug. 2014	1	221	71	651	4288	109	366	506	73	-
WJT030214-2	3 Aug. 2014	1	274	105	874	2957	122	427	537	29	-
WJT040214-1	4 Aug. 2014	0	139	0	383	1146	7	200	130	53	-
C8	2 June 2018	1	8	2	4532	7321	395	4	467	518	13.14
C9	2 June 2018	1	227	3	2847	8117	1614	227	1359	505	9.39
C10	2 June 2018	0	0	68	416	526	131	123	194	60	10.3
C11	2 June 2018	0	25	90	804	1567	300	234	435	101	13.13
C12	2 June 2018	1	1	120	150	795	7	95	177	43	9.8
C13	2 June 2018	1	28	441	4360	5734	987	608	1595	294	7.87
C14	2 June 2018	0	44	86	1582	2588	420	434	826	118	7.73
Mean			96.7	98.6	1659.9	3503.9	409.2	271.8	622.6	179.4	10.2
± SD			± 107.84	± 128.18	± 1659.33	± 2750.64	± 513.29	± 184.39	± 498.27	± 190.47	± 2.22

contained males and/or alate queens. The average number of alate queens in the dry and wet seasons was 30 ± 44 and 97 ± 108 , respectively, while that of males in the dry and wet seasons was 25 ± 58 and 99 ± 128 , respectively. The average number of major and minor workers in the dry season was 1310 ± 1019 and 3973 ± 2728 respectively, while that in the wet season was 1660 ± 1660 and 3504 ± 2751 , respectively. The average number of scale insects in the dry and wet seasons was 150 ± 95 and 174 ± 190 , respectively. Regarding colony size, the number of workers in queenright colonies (7160 ± 3986) did not significantly differ from that of queenless colonies (3635 ± 3293) (Mann-Whitney U test, $U = 67$, $p = 0.09$).

The generalized linear mixed model (GLMM) was utilized to estimate the effect of season, plant length (fixed effect) and colony identity (random effect) on the colony size ($N = 7$ for each season; AIC = 278.5; Table 3). The intercept represents the expected log count of colony size in the dry season. Although the colony size was slightly lower in the wet season, the effect of season on colony size was not statistically significant ($p = 0.493$). Similarly, plant length did not also significantly affect the colony size ($p = 0.795$). The variance of the random effect ($\sigma^2 = 0.6756$) indicates substantial variation at the colony level suggesting that colony identity also influenced colony size (Fig. 5).

The number of major workers in queenright (1768 ± 1555) did not significantly differ from that of queenless colonies (961 ± 678) (Mann-Whitney U test, $U = 57$, $p = 0.393$). In addition, the number of minor workers in queenright (4311 ± 2593) was not significantly different from that of queenless colonies (2675 ± 2686) (Mann-Whitney U test, $U = 66$, $p = 0.115$). Scale insects were found in all colonies, with an average number of 165 ± 147 . A significant linear correlation was observed between the colony size of *C. sirindhornae* and the number of scale insects ($r^2 = 0.39$, $p = 0.003$).

Reproductives and workers were produced in colonies of both the wet and dry seasons. The total number of major and minor workers was not different between seasons (wet season 5164 ± 4245 ; dry season 5283 ± 3663) (Welch two sample

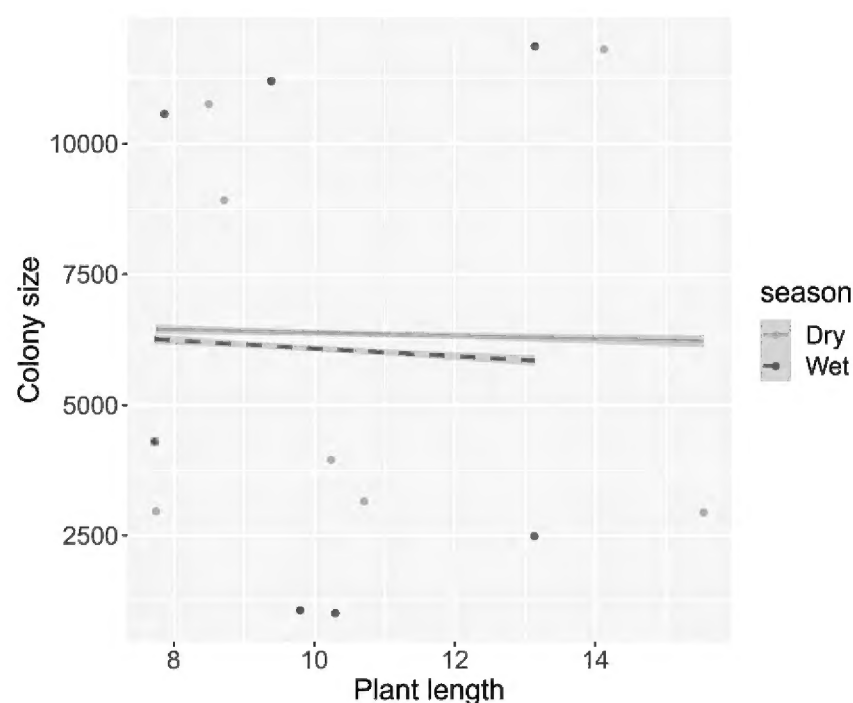


Figure 5. Effect of season and plant length on the colony size of *C. sirindhornae*. The lines show the predicted values based on the fitted Poisson GLMM.

t -test, $t = 0.067$, $df = 18$, $p = 0.9472$; Fig. 6). The number of alate queens and males was not different between the two seasons (Mann-Whitney U test; alate queens, $U = 34$, $p = 0.24$; males, $U = 29$, $p = 0.12$) (Fig. 7); however, when considering alate queens and males combined, the number of reproductives was significantly higher in the wet season (Mann-Whitney U test, $U = 17$, $p = 0.012$). Consistently, the relative number of reproductive pupae in the wet season was significantly larger

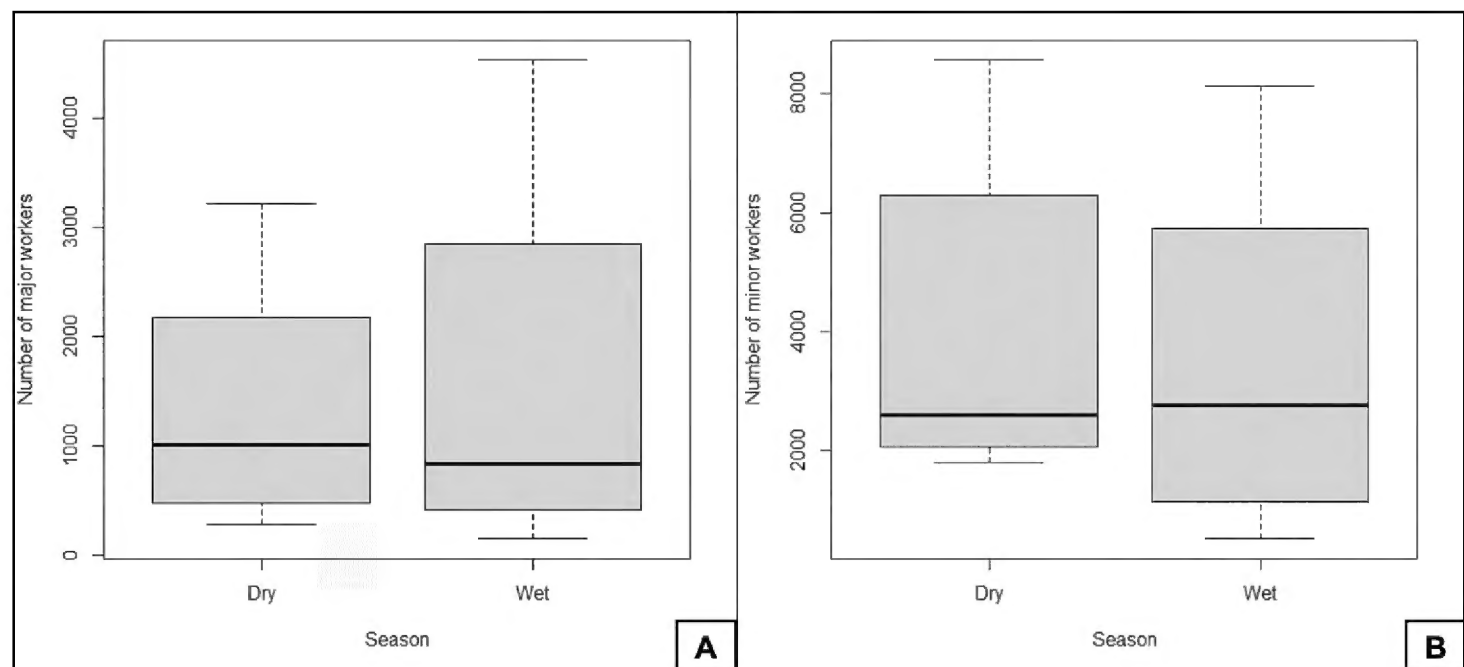


Figure 6. The box plots show the effect of seasons on **A** major worker numbers and **B** minor worker numbers of *C. sirindhornae*.

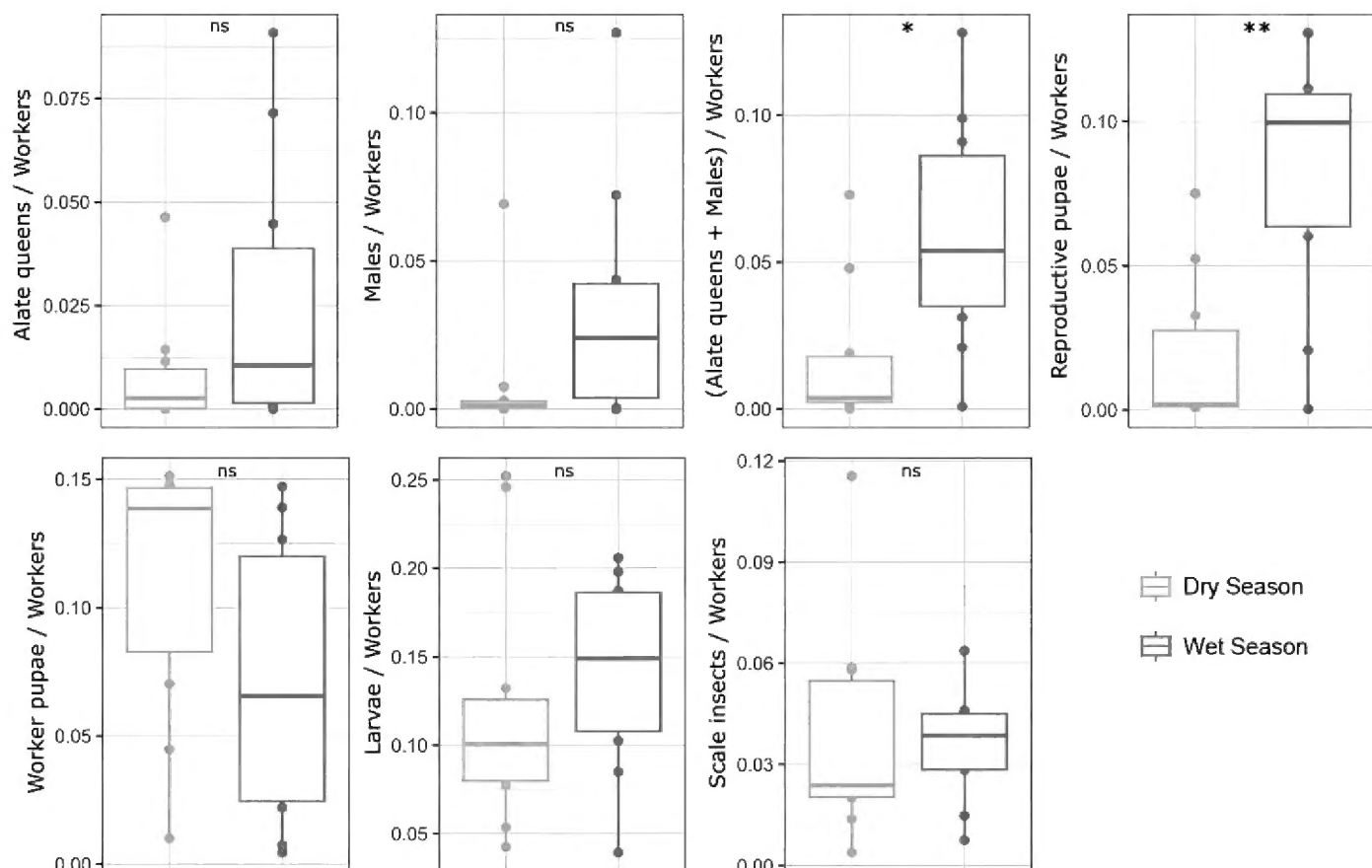


Figure 7. The box plots show the relative comparisons of each colony component, expressed as a ratio between its total number and total number of workers in dissected *C. sirindhornae* colonies, collected in wet and dry seasons. For actual mean + SD numbers of each variable, see Results and Table 1.

than that in the dry season (Mann-Whitney U test, $U = 15$, $p = 0.0068$) (Fig. 7). In contrast, the relative abundance of worker pupae was lower in the wet season than the dry season, even though marginally insignificant (Mann-Whitney U test, $U = 75$, $p = 0.063$) (Fig. 7). The relative abundance of larvae and scale insects did not differ between seasons (Mann-Whitney U test; larvae, $U = 37$, $p = 0.35$; scale insects, $U = 44$, $p = 0.68$) (Fig. 7).

Colony founding

While collecting colonies in the field, we encountered several initial colonies situated on the young stems of *Sphenodesme pentandra*. We often observed the founding dealate queens during the wet season: they chewed on the young stem of the host plant below the node about 1–2 cm, thereby constructing an entrance hole under the node (referred to as “primary hole”). This primary hole, formed by the founding queen, finally led to the formation of a swollen node, and the primary hole was completely closed due to the growth and development of the tree (Fig. 1). The primary hole of the initially established colonies was blocked by the head of founding dealate queens. This behavior was commonly observed when the new colony started. These initially established colonies were notably found more often in the wet season than the dry season, even though we did not record the actual numbers. Initial colonies typically consisted of a single dealate queen, little brood and nanitic workers.

Discussion

A pioneer ant-plant mutualism

The ant genus *Cladomyrma* has been reported to nest in cavities of at least 24 plant species in ten genera from Sundaland and Indochina (Maschwitz et al. 1991; Eguchi and Bui 2007; Moog 2009; Jaitrong et al. 2013) (Table 2). These ant nest in domatia within living shoots, stems, and branches of their host plants. While five species of *Cladomyrma* can be found in various hosts, eight other species (including *C. sirindhornae*) exhibit a preference for specific host plant genera (Table 2). Contrary to most host plants of *Cladomyrma* that inhabit primary or advanced secondary forests (Moog 2009), *S. pentandra* is a pioneer species found in secondary forests, forest edges, and along forest paths in dry evergreen forests. By extension, the nesting habitat of *C. sirindhornae* is unique among *Cladomyrma*. In addition, we found 92% of *S. pentandra* were occupied by *C. sirindhornae*. This high occupation rate is comparable to other associations between myrmecophytes and *Cladomyrma* (100% in *Callerya*, 93–95% in *Drypetes*, 86% in *Luvunga*, and 98% in *Spatholobus*, Moog 2009) and suggests considerably high level of specialisation between the ant and the plant, with likely mutual benefits. Indeed, while myrmecophytes provide a nesting space and indirect nutrition through scale insects to the ants, plant-ants usually benefit their host by protecting them against herbivores, pathogens and plant competitors (Heil and McKey 2003) and, consequently, increase seed set

Table 2. List of geographic regions and host plants colonized by *Cladomyrma* ants. Geographic region; B = Borneo, MP = Malay Peninsula, SU = Sumatra, V = Vietnam, TH = Thailand.

<i>Cladomyrma</i> species	Host plant	Geographic region	References
<i>C. andrei</i>	<i>Callerya nieuwenhuisii</i>	B	Agosti et al. 1999
	<i>Spatholobus oblongifolius</i>	B	Agosti et al. 1999
	<i>Drypetes longifolia</i>	B, MP	Agosti et al. 1999
<i>C. aurochaetae</i>	<i>Neonauclea gigantea</i>	B	Agosti et al. 1999
<i>C. crypteroniae</i>	<i>Crypteronia griffithii</i>	B, MP, SU	Agosti 1991
	<i>C. macrophylla</i>	B	Moog et al. 1998
<i>C. dianeae</i>	<i>Neonauclea borneensis</i>	B	Moog 2009
	<i>N. gigantea</i>	B	Moog 2009
	<i>N. longipedunculata</i>	B	Moog 2009
	<i>N. paracyrtopoda</i>	B	Moog 2009
<i>C. hewitti</i>	<i>Neonauclea longipedunculata</i>	B	Maschwitz et al. 1989
	<i>N. pseudocalycina</i>	B	Moog 2009
<i>C. hobbyi</i>	<i>Spatholobus oblongifolius</i>	B	Agosti et al. 1999
	<i>Drypetes longifolia</i>	B, MP	Donisthorpe 1937
<i>C. maryatiae</i>	<i>Neonauclea</i> spp.	B	Agosti et al. 1999
	<i>Spatholobus oblongifolius</i>	B	Moog 2009
<i>C. maschwitzi</i>	<i>Crypteronia griffithii</i>	B	Moog et al.1998
	<i>C. macrophylla</i>	B	Moog 2009
<i>C. nudidorsalis</i>	<i>Ryparosa fasciculata</i>	MP	Moog et al. 2003
	<i>Drypetes longifolia</i>	B, MP	Moog 2009
<i>C. petalae</i>	<i>Spatholobus bracteolatus</i>	MP	Ridder-Numan and Wiriadinata 1985
	<i>Strychorus vanprukii</i>	MP	Moog 2009
	<i>Luvunga</i> sp.	MP	Moog et al. 2003
	<i>Ryparosa fasciculata</i>	MP	Moog et al. 2003
	<i>Sacara thaipingensis</i>	MP	Maschwitz et al. 1991
	<i>Drypetes longifolia</i>	B, MP	Moog et al. 2003
	<i>Drypetes fusiformis</i>	B, MP	Agosti et al. 1999
<i>C. yongi</i>	<i>D. longifolia</i>	B, MP	Agosti et al. 1999
	<i>Saraca dives</i>	V	Eguchi and Bui 2006
	<i>S. thaipingensis</i>	MP	Moog 2009
<i>C. sirindhornae</i>	<i>Sphenodesme pentandra</i>	TH	This study

Table 3. The GLMM result for the fixed and random effects in the colony size model. An asterisk (*) indicates statistically significant at 0.05 level (N = 7 for each season).

	Fixed effects				Random effects	
	Estimate	Std. Error	z-value	p-value	Groups Name	Variance
(Intercept)	8.836	1.027	8.608	<2e-16*	Colony (Intercept)	0.6756
Season (Wet)	-0.304	0.443	-0.686	0.493		
Plant length	-0.024	0.091	-0.259	0.795		

when ants are present on the plant (Letourneau 1998). However, different plant-ant species can confer different advantages to a same host (Frederickson 2005). *C. sirindhornae* may provide particular benefits that allow *S. pentandra* to grow in open microhabitats. Furthermore, their waste accumulation could supply essential nutrients for the host plant (Leroy 2023). The activities of ants, which are a by-product of their behavior, can considerably benefit the nutrient budget of the host plant (Petitclerc et al. 2012), ultimately benefiting both the plant and the ants by reducing competition. The direct benefits of *C. sirindhornae* to *S. pentandra* remain to be investigated in future studies.

Division of labor and queen fecundity

The colonies of *C. sirindhornae* were large, with an average of 5349 workers. This is comparable to the findings of Moog (2009) who reported several thousand workers in colonies of other *Cladomyrma* species. Approximately 30% (9 to 44%) of workers were major workers, a higher proportion than other ant genera with dimorphic worker castes. For comparison, in *Colobopsis*, another genus of arboreal formicines, the proportion of major workers is 15% in *Colobopsis nipponicus* (Hasegawa 1993), and 20% in *C. impressus* (Walker and Stamps 1986). The high proportion of majors in *C. sirindhornae* suggests that the major caste is crucial to perform specific tasks (e.g. phragmosis) while maintaining a wide behavioral repertoire (Wilson 1984). At least three *Cladomyrma* species (*C. andrei*, *C. maschwitz*, and *C. petalae*) are known to ingest water and regurgitate it outside to prevent their nest from flooding (Moog et al. 1997). Major workers, in virtue of their larger body size, can perform this task more efficiently than minor workers. *C. sirindhornae* may perform such water-bailing behavior during the wet season and benefit from a high proportion of major workers. Behavioral differences between major and minor workers are an interesting perspective for future studies.

According to our data, *C. sirindhornae* from eastern Thailand exhibits monogyny, a trait shared with some species in the Malay Peninsula, Borneo, and Sumatra (*C. cryptata*, *C. andrei*, *C. dianeae*, *C. maschwitz*, and *C. petalae*) (Agosti et al. 1999). Polygyny has only been reported for *C. scopulosa* from northern Vietnam, where founding queens likely cooperate (Eguchi and Bui 2007). The fact that we did not find any founding dealate queen in seven of the twenty dissected colonies (queenless colonies) might be caused probably by the loss of queens during branch collection, as they typically reside near the lower swollen node and may have escaped during cutting. Additionally, worker numbers did not differ significantly between queenright and queenless colonies.

Queens of *C. sirindhornae* had 27 to 37 ovarioles with dense mature oocytes and yellow bodies, while workers had only two ovarioles without yellow bodies. This number is comparable to what is commonly observed in Formicinae (Peeters and Ito 2015) but unexpectedly low considering colony size. Queen ovariole number varies between species and is an indicator of potential reproductive capacity (Lachaud et al. 1999), as a high number of ovarioles means that more eggs can develop and mature concurrently. For example, in Formicinae, queens of *Formica pratensis* have 128 to 180 ovarioles and colonies can have over 30,000 workers (Jensen 1977; Brian 1979) whereas queens of *Myrmoteras iriodum* and *M. jaitrongi* have only four ovarioles and colony size is below twenty (Kaspari and Vargo 1995; Ito et al. 2017). However, queens of *C. sirindhornae* were highly physogastric and contained numerous mature and developing oocytes in their elongated ovaries. Physogastry is associated with a high fecundity and can explain how single founding queens with only ~30 ovarioles can give birth to thousands of workers. One physogastric queen has also been reported in *C. petalae* (Moog 2009), but the reproductive condition of *Cladomyrma* queens remains poorly studied.

Myrmecophytes as an oasis in the dry season

The interspecific interactions between insects and plants are the important success processes of morphological adaptation (Thompson 2013). Ant-plant relationships are particularly important in many tropical communities, standing out as cornerstones when compared to other animal groups (Hölldobler and Wilson 1990; Blüthgen et al. 2000; Rosumek et al. 2009). Myrmecophytes act as a refuge for herbivores during the dry season. Plants that experience climate change, water stress, or nutritional deficiencies are more vulnerable to herbivory, making them more attractive to herbivores (Edwards and Wratten 1981; Bezemer and Jones 1998; Agrell et al. 2006). Martins et al. (2020) reported that the highest proportion of herbivory occurred during the dry season, a period that abundance of ants also increased. The myrmecophilous herbivorous species are able to occupy the enemy-free space in the host plant due to the benefit from the protection by the associated ants (Pierce et al. 2002). Ants gain benefits not only from the extrafloral nectar but also from the secretions produced by the larvae of myrmecophilous herbivores. Meanwhile, the plants lose protection from other herbivores, as they are being consumed by larvae, leading to a significant increase in the herbivorous area (Martins et al 2020). During the dry season, plants receive protection from ants and, in return, provide them with nourishment from both plant resources and herbivorous insects, serving as an important food source when food is scarce.

In case of colonies of *C. sirindhornae* here, they produced more reproductives during the wet season. As the development of reproductives requires more energy than workers, this result may indicate a shortage of resources in the dry season. However, no differences in colony size, number of worker pupae, larvae and scale insects were observed between the wet and the dry seasons. This result suggests that the dry season has negligible effects on colony growth and the host plant. Instead, the variation in production of reproductives could simply mean that mating flight exclusively takes place in the wet season. Indeed, in the field, we consistently found more founding queens in the wet season than the dry season, chewing a hole on the young stem of their host or using their head to seal the nest entrance. Reproductives need to leave their host plant to mate, hence favourable abiotic parameters such as moderate temperature and high humidity may be crucial for successful mating and colony founding.

During the dry season, while *C. sirindhornae* colonies were proliferating, many ground-dwelling ant colonies (e.g. Ponerinae) were found without brood at the same locations (pers. obs.). This contrast is analogous to an oasis in the desert: ant-plants buffer harsh environmental conditions and provide a nesting space with humidity and even nutrition through scale insects and food-bodies year-round. Although honeydew is a beneficial food source, it is nitrogen-poor and likely insufficient for colony growth (Helms and Vinson 2008). Plant-ants can also get proteins from bacteria, fungi, and herbivores that attack their hosts (Defosse et al. 2011; Arcila Hernández et al. 2017). As a consequence, they do not need to leave the domatia, except for the reproductives

that can be produced specifically in the wet season when conditions outside are favorable. Ants and plants have coexisted together for at least 140 million years (Moreau et al. 2006) and developed a large range of mutualistic interactions. The role of abiotic factors in the evolution of ant-plant mutualisms is undeniable (Kersch and Fonseca 2005; Mayer et al. 2014) but remains to be investigated on a large scale.

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